Transactions of the Royal Society of S. Aust. (2004), **128**(2), 175-185.

CESTODE PARASITES OF TREE KANGAROOS (*DENDROLAGUS* SPP.: MARSUPIALIA), WITH THE DESCRIPTION OF TWO NEW SPECIES OF *PROGAMOTAENIA* (CESTODA: ANOPLOCEPHALIDAE)

by I. BEVERIDGE* & P. M. JOHNSON†

Summary

BEVERIDGE, I. & JOHNSON, P. M. (2004). Cestode parasites of tree kangaroos (*Dendrolagus* spp.: Marsupialia), with the description of two new species of *Progamotaenia* (Cestoda: Anoplocephalidae). *Trans. R. Soc. S. Aust.* **128**(2), 175-185, 30 November, 2004.

Two new species of *Progamotaenia* Nybelin, 1917 are described from tree kangaroos: *P. dendrolagi* sp. n. from the small intestines of *Dendrolagus bennettianus* De Vis, 1887 and *D. lumholtzi* Collett, 1884 from north-eastern Queensland, and *P. irianensis* sp. n. from the intestine of *D. dorianus* Ramsay, 1883 from Irian Jaya. A re-description of *P. wallabiae* Beveridge, 1985, from *D. dorianus*, a new host for the genus, is given. *P. dendrolagi* is highly host specific, being restricted to tree kangaroos, while *P. wallabiae* occurs also in scrub wallabies of the genus *Dorcopsis* Schlegel & Mueller, 1842 from the island of New Guinea. The phylogenetic relationships of *P. irianensis* with congeners are not clear. The life cycles of the cestodes are discussed in relationship to the arboreal nature of the hosts and the presumed use of terrestrial oribatoid mites as intermediate hosts.

KEY WORDS: Cestoda, Anoplocephalidae, *Progamotaenia*, *Dendrolagus*, tree kangaroos, Macropodidae, new species.

Introduction

The helminth parasites of tree kangaroos (*Dendrolagus* spp.) are poorly known (Spratt *et al.* 1991), with most parasite records being based upon opportunistic collecting involving one or two host specimens. A study of a series of seven *D. lumholtzi* Collett, 1884, from north-eastern Queensland (Beveridge *et al.* 1992) revealed a relatively depauperate helminth community, a fact attributed to the arboreal nature of the host compared with a predominantly terrestrial mode of transmission of most of the helminth parasites of macropodid marsupials (Beveridge & Spratt 1996). A recent examination of a limited number of specimens of *Dendrolagus* spp. from Irian Jaya (Flannery *et al.* 1996) has suggested that that some species may harbour a more complex community of helminths than described in previous publications, with some species of helminths occurring in considerable numbers.

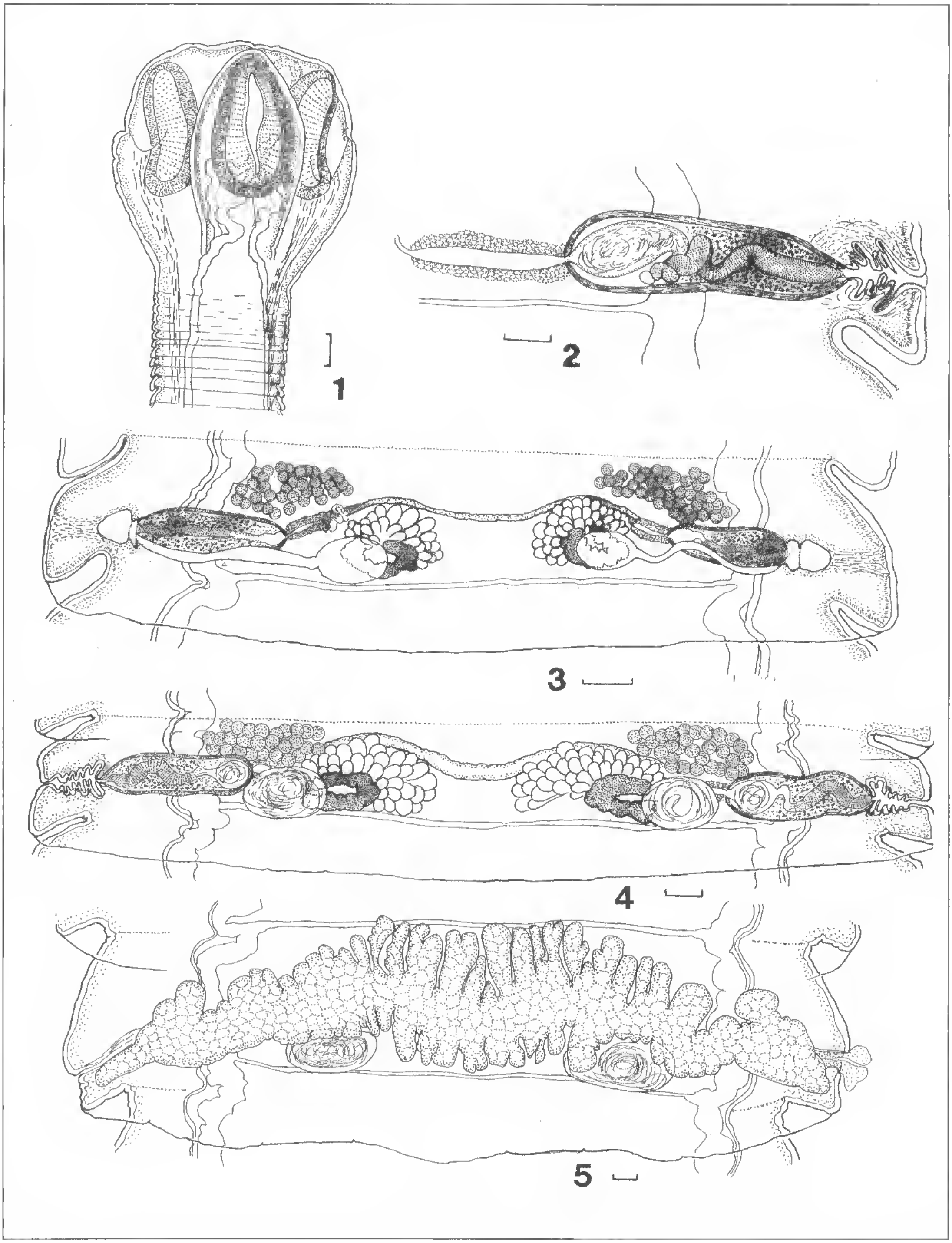
Although the cestode genus *Progamotaenia* Nybelin, 1917 is abundant in many macropodid species (Beveridge 1976, 1978b, 1980, 1985; Beveridge & Thompson 1979; Turni & Smales 1999; Beveridge & Turni 2003), records of the genus from tree kangaroos are few. Löser (1965) in a study of the histology of the female genital glands of cestodes reported the occurrence of *P. zschokkei* (Janicki, 1906) in *D. ursinus* Mueller, 1840 from a European zoo, while Spratt *et al.* (1991) and Beveridge *et al.* (1992) reported *P. zschokkei* from *D. lumholtzi* in north-eastern Queensland. Spratt *et al.* (1991) also reported the presence of an undescribed species of *Progamotaenia* in *D. bennettianus* De Vis, 1887 from Queensland, while Flannery *et al.* (1996) reported two species of cestodes, *P. wallabiae* Beveridge, 1985 and *P.* cf. *dorcopsis* Beveridge, 1985, from *D. dorianus* Ramsay, 1883 from Irian Jaya. The fragmentary data available to date therefore suggest that tree kangaroos might harbour a number of species of anoplocephalid cestodes.

In this report, the species of cestodes present in tree-kangaroos are reviewed and two new species are described, one from northern Queensland and one from Irian Jaya. A further species found in tree kangaroos, but formerly known only from scrub wallabies, *P. wallabiae*, is re-described and the associations between hosts and parasites are considered.

Materials and Methods

Cestodes obtained were from animals which had been collected for other purposes. Specimens of *D. lumholtzi* were obtained as road-kills and frozen prior to examination. At autopsy, cestodes were washed in water and fixed in AFA (Pritchard & Kruse 1982). Individuals of *D. dorianus* were collected for museum specimens and the entire gastrointestinal tracts had been fixed in formalin prior to examination. Cestodes were removed,

* Department of Veterinary Science, University of Melbourne, Parkville Vic. 3052.
† Queensland Parks and Wildlife Service, Townsville, Qld 4810.



Figs 1-5. *Progamotaenia dendrolagi* sp. nov. 1. Scolex. 2. Cirrus sac and genital atrium. 3. Premature segment prior to patency of genital atria, showing vaginae extending to atrial primordia. 4. Mature segment showing patency of atria, sperm in seminal receptacles and disappearance of vaginae. 5. Pregravid segments showing single uterus with numerous anterior and posterior diverticula. All illustrations from holotype. Scale bars = 0.1 mm.

washed in water and stored in 70% ethanol.

Cestodes were stained in Celestine blue, dehydrated in ethanol and cleared in methyl salicylate. In thick or dark specimens, the cleared cestodes were allowed to harden in methyl salicylate and the tegument and longitudinal muscle layers removed with fine forceps to reveal the medullary organs. In some instances, hand-cut transverse sections were prepared of mature or gravid segments. Cestodes were mounted in Canada balsam. Parts of new species of cestodes were embedded in paraffin, serially sectioned at a thickness of 10 μm and the sections stained with haematoxylin and eosin.

Drawings were made using a drawing tube attached to an Olympus BH microscope. Measurements were made with an ocular micrometer or a ruler and are presented throughout the paper in millimetres as the mean followed, in parentheses, by the range and the numbers of measurements made (n=).

Type specimens have been deposited in the South Australian Museum, Adelaide (SAM).

Host nomenclature follows Groves & Flannery (1989), Spratt *et al.* (1991) and Flannery *et al.* (1996).

Progamotaenia dendrolagi sp. nov.
(FIGS 1-5)

Synonyms: *Progamotaenia* sp. nov. of Spratt *et al.* 1991, p. 62 (*Dendrolagus bennettianus*); *Progamotaenia zschokkei* (Janicki, 1906) of Spratt *et al.* (1991), Beveridge *et al.* (1992) (*Dendrolagus lumholtzi*).

Holotype: From *Dendrolagus bennettianus* De Vis, 1887, Bargoo Creek, Mount Windsor State Forest, Queensland (23° 38′ S 141° 40′ E), 19.ix. 1986, coll. G. Richards, SAM AHC 22654.

Paratypes: From *Dendrolagus lumholtzi* Collett, 1884 : Queensland : 3 specimens, Mount Baldy State Forest, (17° 17′ S 145° 27′ E), 7.viii.1991, coll. P.M. Johnson (SAM AHC 28511-3); 1 specimen, Herberton (17° 23′ S 145° 23′ E), 1.i.1990, coll. P.M. Johnson (SAM AHC 28514-5); fragments of 1 specimen, Malanda (17° 21′ S 145° 36′ E), 1993, coll. P.M. Johnson (SAM AHC 28516); 2 specimens, Palmerston (17° 32′ S 145° 40′ E), coll. 16.xii.1976, P.M. Johnson (SAM AHC 12231, 22132), (serial sections SAM AHC 28517) (10 slides).

Site in host: Small intestine

Description

Small cestodes, holotype 54 long, 4 wide, composed of 170 segments; paratypes 28 – 60 (43, n = 3) long, width 4 – 6 (5, n = 3). Scolex prominently 4-lobed, 0.76 in diameter in holotype, 0.74 – 1.21 (1.04, n = 4) in diameter in paratypes, with oval suckers 0.39-0.42 (0.41, n = 3) long by 0.17 – 0.24 (0.21, n = 3) wide in holotype, 0.30 – 0.38 (0.35, n = 10) long by 0.20 – 0.33 (0.27, n = 10) wide in paratypes. Neck absent or very short. Segments transversely elongate, with prominent velum overhanging subsequent segment; posterior border of velum straight or slightly undulate; as segments increase in size along strobila, velum covers 1/2 to 2/3 of succeeding segment. Premature segments 0.27 – 0.31 (0.29, n = 5) long, 1.56 – 1.01 (1.72, n = 5) wide, velum 0.05 – 0.13 (0.09, n = 5) long in holotype; 0.28 – 0.44 (0.37, n = 5) long, 2.57 – 3.13 (2.95, n = 5) wide, velum 0.20 – 0.24 (0.22, n = 5) long in paratypes. Mature segments 0.29 – 0.32 (0.30, n = 5) long, 1.95 – 2.65 (2.39, n = 5) wide, velum 0.08 – 0.10 (0.09, n = 5) long in holotype; 0.39 – 0.47 (0.42, n = 5) long, 3.04 – 3.90 (3.50, n = 5) wide, velum 0.17 – 0.26 (0.22, n = 5) long in paratypes. Pregravid segments 0.47 – 0.61 (0.52, n = 5) long, 3.12 – 3.82 (3.56, n = 5) wide, velum 0.19 – 0.26 (0.23, n = 5) in holotype; 0.35 – 0.66 (0.51, n = 5) long, 4.91 – 5.93 (5.41, n = 5) wide, velum 0.27 – 0.43 (0.35, n = 5) long in paratypes. Genital pores paired, in middle of lateral segment margins. In premature segments, genital atrium circular in dorso-ventral views, not patent; in mature segments, genital atrium consists of narrow central passage with numerous anterior and posterior diverticula; when everted, cirrus extrudes from genital papilla formed by everted genital atrium. Cirrus sac elongate, with thick muscular wall, extending beyond osmoregulatory canals into medulla. Cirrus sac in holotype 0.37 – 0.45 (0.41, n = 5) long by 0.10 – 0.14 (0.12, n = 5) in mature segments, 0.58 – 0.68 (0.63, n = 5) long by 0.16 – 0.20 (0.17, n = 5) wide in pregravid segments; in paratypes 0.39 – 0.61 (0.50, n = 5) long by 0.12 – 0.16 (0.14, n = 5) wide in mature segments, 0.51 – 0.64 (0.58, n = 5) long by 0.17 – 0.21 (0.19, n = 5) wide in pregravid segments. Cirrus armed distally with numerous, regularly-arranged spines; width of cirrus diminishes proximally with similar reduction in size of spines; most proximal region of cirrus unarmed, leads into sub-circular or fusiform internal seminal vesicle; cirrus sac between distal extremity and internal vesicle filled with densely-staining gland cells. Internal seminal vesicle in holotype 0.09 – 0.16 (0.12, n = 5) long by 0.08 – 0.09 (0.08, n = 5) in mature segments, 0.16 – 0.28 (0.20, n = 5) long by 0.12 – 0.16 (0.13, n = 5) wide in pregravid segments; in paratypes 0.12 – 0.18 (0.16, n = 5) long by 0.08 – 0.10 (0.09, n = 5) in mature segments, 0.12 – 0.20 (0.19, n = 5) long by 0.08 – 0.20 (0.12, n = 5) wide in pregravid segments.

External seminal vesicle clearly visible only in post-mature segments, elongate, extends medially and anteriorly from proximal pole of cirrus sac, covered with layer of glandular cells; external seminal vesicle 0.21 – 0.27 (0.25, n = 5) long by 0.05 – 0.08 (0.07, n = 5) in holotype, 0.31 – 0.47 (0.38, n = 5) long by 0.07 – 0.12, n = 5) wide in paratypes; vas deferens arises from proximal pole of external seminal vesicle. Testes invariably arranged in two completely separate groups extending from ventral osmoregulatory canals to level of seminal receptacle; 3 to 8 rows of testes in antero-posterior direction; 3 to 4 layers in dorso-ventral plane; 36 – 55 (43, n = 5) per group in holotype; 35 – 47 (43, n = 5) per group in paratypes. Testis diameter 0.043 – 0.059 (0.050, n=10) in holotype, 0.055 – 0.070 (0.062, n = 10) in paratypes.

Vagina tubiform, opening to genital atrium posterior to cirrus sac; connection between vagina and genital atrium clearly visible in premature segments prior to patency of genital atrium; once genital atrium becomes patent, distal vagina atrophies and becomes inapparent. Vagina leads to ovoid seminal receptacle on posterior margin of segment medial to cirrus sac; receptacle empty prior to patency of genital atrium, filled with sperm immediately after genital atrium becomes patent. Seminal receptacle in holotype 0.21 – 0.27 (0.24, n = 5) long by 0.15 – 0.20 (0.16, n = 5) wide in mature segments, 0.20 – 0.41 (0.34, n = 5) long by 0.16 – 0.27 (0.21, n = 5) wide in gravid segments; in paratypes 0.26 – 0.51 (0.37, n = 5) long by 0.16 – 0.27 (0.21, n = 5) wide in mature segments, 0.37 – 0.55 (0.48, n = 5) long by 0.12 – 0.23 (0.19, n = 5) wide in gravid segments. Ovary flabelliform, with oöcapt near medial pole of seminal receptacle; ovary on ventral aspect of medulla. Ovary in holotype 0.16 – 0.23 (0.20, n = 5) long, 0.31 – 0.45 (0.40, n = 5) wide; in paratypes 0.21 – 0.27 (0.23, n = 5) long, 0.37 – 0.59 (0.44, n = 5) wide. Vitellarium horseshoe-shaped, posterior and dorsal to oöcapt; in holotype 0.08 – 0.10 (0.09, n = 5) long by 0.20 – 0.23 (0.21, n = 5) wide; in paratypes 0.09 – 0.12 (0.11, n = 5) long by 0.21 – 0.28 (0.23, n = 5) wide. Mehlis' gland spherical, visible only in paratypes, situated in U formed by vitellarium, 0.09 – 0.12 (0.11, n = 5) in diameter. Uterus single in each segment situated anterior to ovaries; immature uterus tubiform, extending laterally only to proximal poles of cirrus sacs; in pregravid segments, uterus develops numerous anterior and posterior diverticula, extends laterally, dorsal to osmoregulatory canals, almost reaching postero-lateral corners of segments. No gravid specimens present; eggs in all available specimens immature. Paired osmoregulatory canals present; ventral canal larger, 0.02 – 0.17 in diameter; dorsal canal external to ventral, much narrower, 0.04 – 0.11 in diameter; transverse canal, 0.02 – 0.04 in diameter connects ventral canals at posterior margin of each segment. Inner longitudinal musculature weakly developed, consisting of elongate bundles of up to 12 muscle fibres in medial zone of cortex; transverse muscles form distinct band at cortico-medullary junction; dorso-ventral muscles prominent, arranged as numerous individual fibres crossing cortex and medulla.

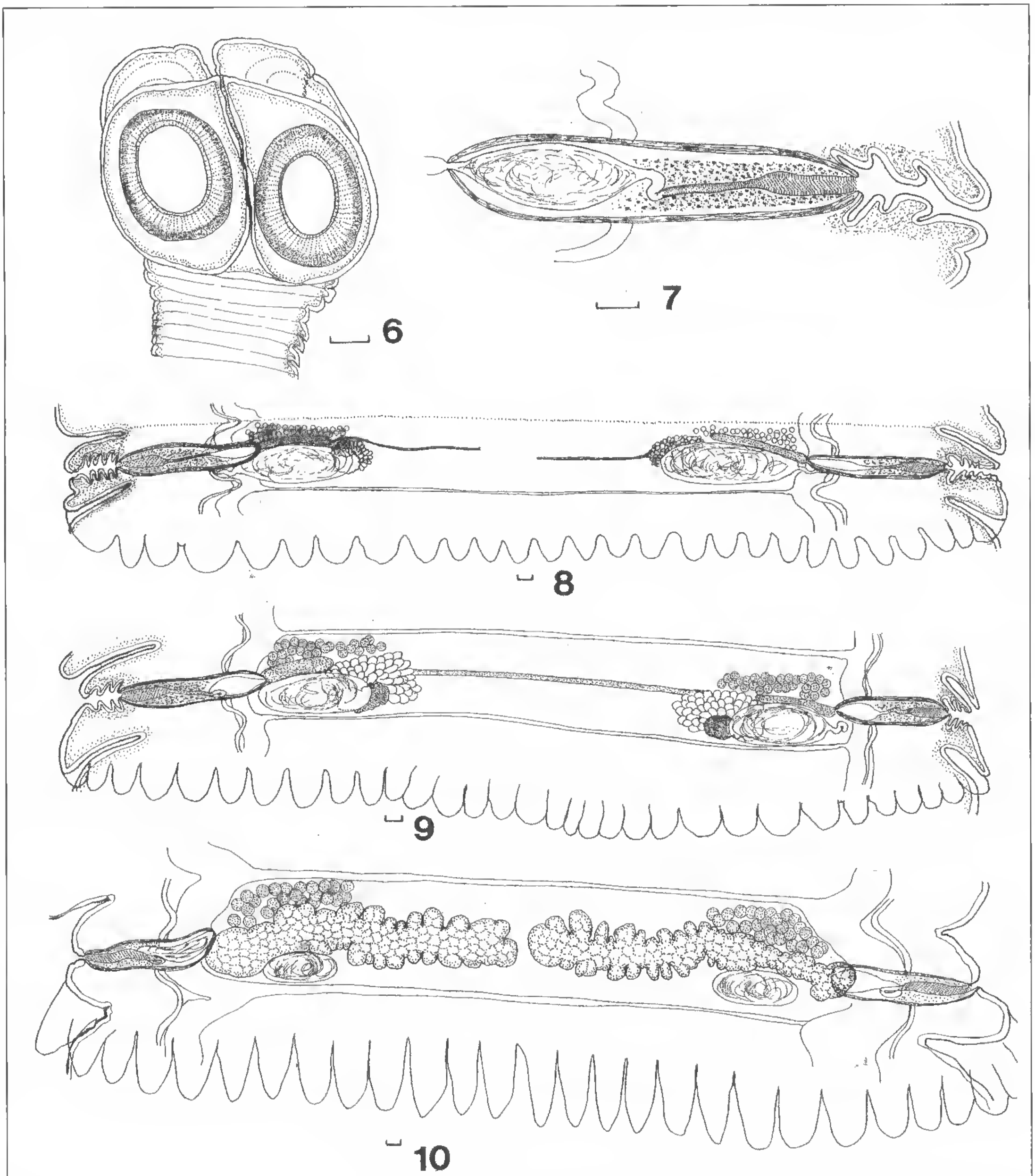
Development of segments in holotype : genitalia fully formed by segment 55; genital atrium becomes patent and sperm appears in seminal receptacle in segment 70; uterus commences filling in segment 80; ovary involuted with remnants of vitellarium still present by segment 120; anterior and posterior diverticula of uteri present in segment 125; total number of segments 170.

Remarks

Most species of *Progamotaenia* possess two uteri per segment. Schmidt (1986) separated those species with a single uterus into two genera *Adelataenia* Schmidt, 1986 and *Wallabicestus* Schmidt, 1975, neither of which was accepted by Beveridge (1994). The species described above is therefore allocated to *Progamotaenia* based on the definition of the genus by Beveridge (1994) which includes species with both single and paired uteri. Species with a single uterus are *P. effigia* Beveridge, 1976, *P. ewersi* (Schmidt, 1975), *P. villosa* (Lewis, 1914) and *P. zschokkei* (Janicki, 1906).

The specimens described above differ from *P. villosa* and *P. zschokkei* in lacking a distinctly fimbriated velum and differ from *P. effigia* and *P. ewersi* in having the testes distributed in two distinct groups rather than in a single continuous band across the medulla. In addition they differ from *P. effigia* in having an external seminal vesicle covered with glandular cells (lacking in *P. effigia*) and in infecting the small intestine rather than the bile duct, as is the case with *P. effigia*. They further differ from *P. ewersi* in lacking a distal vagina surrounded by prominent layers of glandular cells and in having the vagina atrophy following insemination of the proglottis. The specimens therefore represent a new species for which the name *P. dendrolagi* is proposed.

The description of *P. dendrolagi* is based primarily upon a single, well-preserved specimen from *D. bennettianus*, in which most, but not all features of its morphology can be observed. The type series is completed by a number of specimens from *D. lumholtzi*. The latter specimens are poorly preserved and while they are not differentiable from the holotype, are insufficient on their own to permit a full description. The description of the new species is therefore based on a collection of specimens from



Figs 6-10. *Progamotaenia irianensis* sp. nov. 6. Scolex. 7. Cirrus sac and genital atrium. 8. Premature segment showing patency of genital atria, filling of seminal receptacles with sperm but poor development of both male and female genitalia within segment. 9. Mature segment with fully developed genitalia and single uterus. 10. Pregravid segment with fully developed uteri. Drawings from types. Scale bars = 0.1 mm.

two host species within the same genus and may need to be reviewed if and when more extensive series of cestode specimens from these two host species become available. One feature of the new species which warrants comment is the development of the genital atrium which becomes patent only in mature segments. This developmental feature has only been observed previously in *P. capricorniensis*

Beveridge & Turni, 2003 from the black-stripe wallaby, *Macropus dorsalis* (Gray, 1837), from central Queensland (Beveridge & Turni 2003), but provides an additional developmental character distinguishing the new species from all other congeners.

Progamotaenia irianensis sp. nov.
(FIGS 6-10)

Synonyms: *Progamotaenia* cf *dorcopsis* of Flannery *et al.*, 1996, p. 187.

Holotype: From *Dendrolagus dorianus stellarum* Flannery & Seri, 1990, Gunung Ki, Tembagapura, Irian Jaya, Indonesia (4° 05′ S, 137° 06′ E), collected 19.v.1994 by T. Flannery, SAM AHC 28512.

Paratypes: 2 specimens, same data SAM AHC 28519-24; serial sections SAM AHC 28525 (5 slides), spirit material SAM AHC 32180.

Site in host: Small intestine.

Description

Large, robust cestodes, holotype 95 long, 6 wide, composed of 315 segments; paratype 67 long, width 5.0. Scolex prominently 4-lobed, 0.70 – 0.80 (0.75, n = 3) in diameter, with 4 oval suckers 0.36 – 0.44 (0.40, n = 4) long by 0.23 - 0.31 (0.26, n = 4) wide. Neck absent or very short. Segments transversely elongate, with prominent velum overhanging subsequent segment; posterior border of velum undulate with 29 (27 – 32, n = 5) blunt, linguiform projections overhanging succeeding segment on both dorsal and ventral aspects of strobila; as segments increase in size along strobila, velum covers ½ to ⅔ of succeeding segment. Premature segments 0.18 – 0.43 (0.28, n = 5) long, 3.86 – 4.17 (4.02, n = 5) wide, velum 0.16 – 0.29 (0.20, n = 5) long; mature segments 0.27 – 0.68 (0.45, n = 5) long, 4.25-5.15 (4.72, n = 5) wide, velum 0.23 – 0.44 (0.33, n = 5) long; pregravid segments 0.49 – 0.62 (0.56, n = 5) long, 4.91 – 5.85 (5.38, n = 5) wide, velum 0.29 – 0.55 (0.40, n = 5) long. Genital pores paired, in middle of lateral segment margins. In pre-mature segments, genital atrium circular in dorso-ventral views, not patent; in mature segments, genital atrium consists of narrow central passage with numerous anterior and posterior diverticula. Cirrus sac elongate, with thick muscular wall, extending just beyond osmoregulatory canals into medulla, 0.59 – 0.80 (0.69, n = 5) long, 0.15 – 0.17 (0.16, n = 5) wide in mature segments, 0.69 – 0.94 (0.81, n = 5) long, 0.19 – 0.25 (0.21, n = 5) wide in pregravid segments. Cirrus almost straight or with single flexure; armed distally with numerous, regularly-arranged spines; distal segment of cirrus greatly dilated; width of cirrus diminishes proximally with similar reduction in size of spines; most proximal region of cirrus unarmed, leads into ellipsoidal or fusiform internal seminal vesicle 0.18 – 0.25 (0.23, n = 5) by 0.08 – 0.13 (0.10, n = 5) in mature segments, 0.34 – 0.44 (0.40, n = 5) by 0.15 – 0.17 (0.16, n = 5) in pregravid segments ; cirrus sac between distal extremity and internal vesicle filled with densely-staining gland cells. External seminal vesicle clearly visible only in post-mature segments, elongate, extends medially and anteriorly from proximal pole of cirrus sac, along anterior border of seminal receptacle; covered with layer of glandular cells, 0.33 – 0.51 (0.41, n = 5) by 0.06 – 0.09 (0.08, n = 5); vas deferens arises from proximal pole of external seminal vesicle. Testes invariably arranged in two completely separate groups extending from ventral osmoregulatory canals to level of medial pole of seminal receptacle; 25 – 47 (37, n = 5) per group; 1 to 4 rows of testes in antero-posterior direction; 3-5 layers in dorso-ventral plane, 0.040 – 0.060 (0.050, n = 10) in diameter.

Vagina tubiform, opening to genital atrium posterior to cirrus sac; connection between vagina and genital atrium clearly visible in pre-mature segments prior to patency of genital atrium; once genital atrium becomes patent, distal vagina atrophies and becomes inapparent. Vagina leads to ovoid seminal receptacle on posterior margin of segment medial to cirrus sac and dorsal to female genitalia, 0.35 – 0.62 (0.48, n = 5) by 0.20 – 0.27 (0.24, n = 5); receptacle empty prior to patency of genital atrium, filled with sperm immediately genital atrium becomes patent. Ovary flabelliform, 0.24 – 0.33 (0.27, n = 5) by 0.47 – 0.78 (0.67, n=5), ventral, with oocapt near medial pole of seminal receptacle; ovary on ventral aspect of medulla. Vitellarium horseshoe-shaped, posterior and dorsal to oöcapt, 0.11 – 0.16 (0.12, n = 5) by 0.30 – 0.39 (0.34, n = 5). Mehlis' gland spherical, situated in U of vitellarium. Uterus usually paired in each segment, occasionally only a single uterus present; situated anterior to ovaries; immature uterus tubiform, extending laterally only to proximal poles of cirrus sacs; in pregravid segments, uterus develops numerous anterior and posterior diverticula, extends laterally dorsal to osmoregulatory canals, but does not cross canals. No gravid specimens present; eggs in all available specimens immature. Paired osmoregulatory canals present; ventral canal larger, 0.086 – 0.094 in diameter in mature segments, 0.094 – 0.24 in post-mature segments; dorsal canal external to ventral, much narrower, 0.016 – 0.031 in diameter in mature segments, 0.016 – 0.047 in diameter in post-mature segments; transverse canal connects ventral canals at posterior margin of each segment; tiny accessory osmoregulatory canal observed medial to ventral canal in sections; transverse canal connects accessory canals at posterior margin of segment. Inner longitudinal musculature strongly developed, consisting of bundles of up to 20 muscle fibres concentrated in medial zone of cortex; transverse muscles form distinct band at cortico-medullary junction; dorso-ventral muscles prominent, arranged as numerous individual fibres crossing cortex and medulla.

Development of segments in holotype: genitalia fully formed by segment 100; genital atrium becomes patent in segment 120 and sperm appears in seminal receptacle in segment 123; uterus commences filling in segment 170; ovary involuted with remnants of vitellariun still present by segment 210; total number of segments 315.

Remarks

The species described above is based on few specimens which are fragmented and imperfectly preserved. However, because of the difficulty of obtaining material from tree kangaroos occurring at high altitudes in Irian Jaya, the description of a new species based on these specimens, albeit incomplete, is considered justified.

The species is characterised by two uteri, a prominently fimbriated velum and testes distributed exclusively in two groups. In a small number of segments, a single uterus is present, but the same phenomenon has been described previously in *P. festiva* by Beveridge (1976, p. 54) and is common in species of the anoplocephalid genus *Mosgovoyia* Spasskii, 1951 from lagomorphs (Beveridge 1978a).

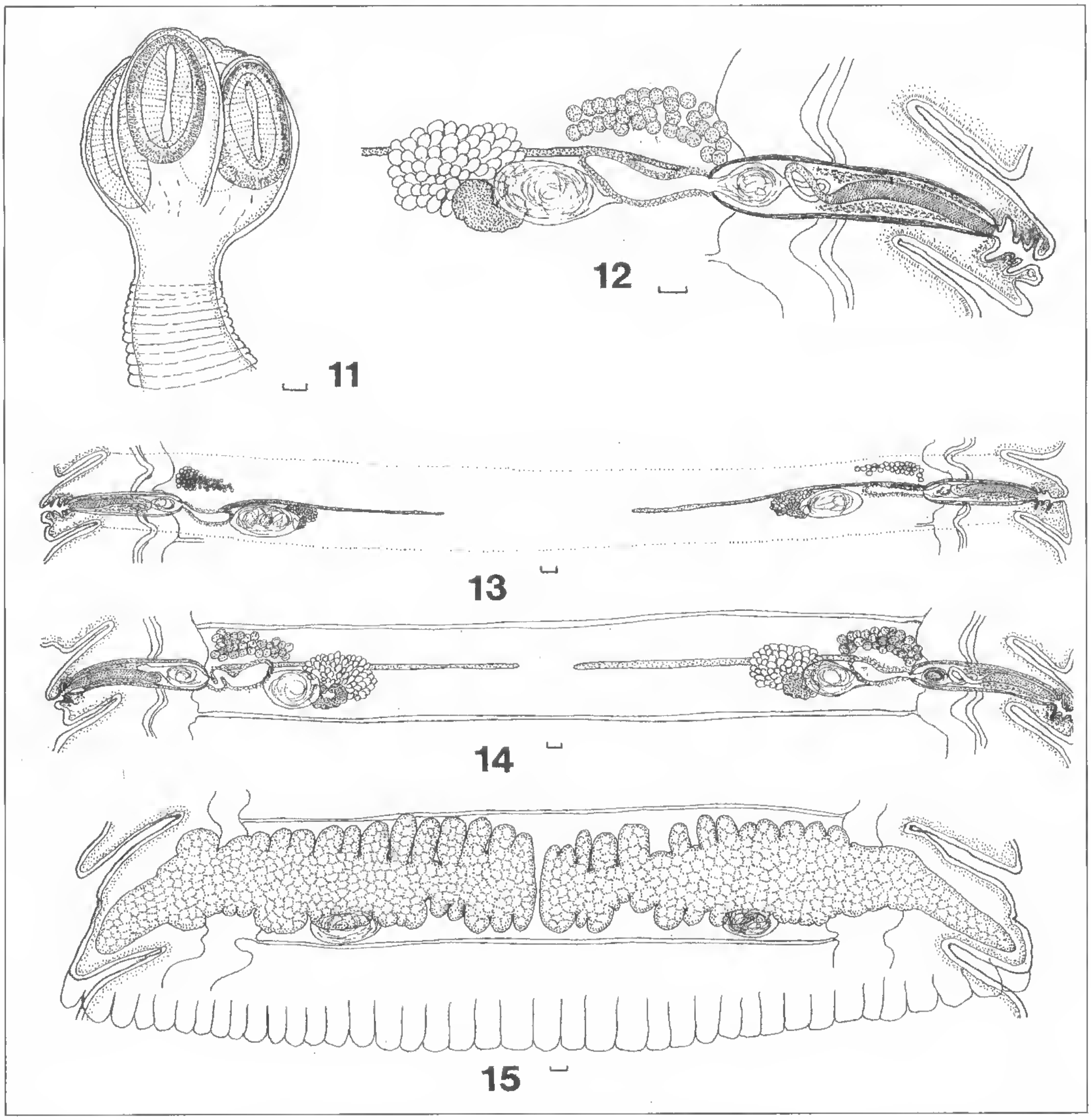
Species with a similar combination of characters are: *P. thylogale* Beveridge & Thompson, 1979, *P. lagorchestis* (Lewis, 1914), *P. spearei* Beveridge, 1980, *P. dorcopsis* Beveridge, 1985 and *P. queenslandensis* Beveridge, 1980. Of these species, *P. queenslandensis* frequently has the testes distributed in a single band as well as in two groups (Beveridge 1985). The species described above has an external seminal vesicle with a distinctive covering of glandular cells, thereby distinguishing it from *P. spearei*. The projections of the velum are distinctly linguiform in this species, differentiating them from the triangular projections seen in *P. lagorchestis*, *P. dorcopsis* and *P. queenslandensis*. The number of projections of the velum (27-32) also distinguishes the specimens from *P. thylogale* (18-21), *P. dorcopsis* (13-17) and *P. queenslandensis* (17-20) (Beveridge 1985). The number of testes per group (25-47) distinguishes the specimens from *P. thylogale* (50) and *P. dorcopsis* (18-25) (Beveridge 1985), while the distribution of the testes from the osmoregulatory canals to anterior to the aporal pole of the seminal receptacle distinguishes the species from *P. lagorchestis* in which the testes extend only to the poral pole of the seminal receptacle (Beveridge & Thompson 1979). The cestodes from *D. dorianus* have a similar number of linguiform projections to the velum as *P. capricorniensis*, but in the latter species a single uterus is present (Beveridge & Turni 2003). A singular feature of these specimens appears to be the fact that the uteri do not cross the osmoregulatory canals, even in near gravid segments. This character is unusual within the genus but has been reported in *P. zschokkei* (see Beveridge 1976, p. 67). In *P. spearei*, the uteri only cross the canals in the last few segments (Beveridge 1980). As fully gravid specimens were not available in the current series of specimens examined, it may be prudent not to rely on this feature as a specific character, but given the state of development of the specimens available, it seems unlikely that a major development of the uterus will occur beyond the 300th segment. Consequently, the species described above can be easily distinguished from all known congeners. It is therefore considered to be new and the specific name is given because these are the first new representative of the genus described from Irian Jaya, Indonesia.

Progamotaenia wallabiae Beveridge, 1985 (FIGS 11-15)

Material examined: 3 specimens from *Dendrolagus dorianus stellarum* Flannery & Seri, 1990, Gunung Ki, Tembagapura, Irian Jaya. Indonesia (4° 05′ S, 137° 06′ E), collected 19.v.1994 by T. Flannery, SAM AHC 28526-8; spirit material SAM AHC 32181.

Description

Large, robust cestodes, to 108 long, 5.0 wide, composed of 225 segments. Scolex prominently 4-lobed, 0.99 – 1.17 in diameter, with oval suckers, 0.62 – 0.70 (0.64, n = 4) by 0.35 – 0.47 (0.40, n = 4). Neck absent or very short, up to 0.23 long. Segments transversely elongate, with prominent velum overhanging subsequent segment; posterior border of velum very slightly undulate with c. 30-35 blunt-tipped lobes, not separated into individual projections, overhanging succeeding segment on both dorsal and ventral aspects of segment; as segments increase in size along strobila, velum covers 1/2 to 2/3 of succeeding segment. Premature segments 0.23 – 0.39 (0.29, n = 5) long by 3.82 – 4.91 (4.42, n = 5) wide, velum 0.09 – 0.18 (0.12, n = 5) long; mature segments 0.37 – 0.56 (0.44, n = 5) long by 4.52 – 6.40 (5.63, n = 5) wide, velum 0.21 – 0.27 (0.23, n = 5) long; pregravid segments 0.620 – 0.82 (0.73, n = 5) long by 4.29 – 5.30 (5./00, n = 5)



Figs 11-15. *Progamotaenia wallabiae* Beveridge, 1985. Specimens from *Dendrolagus dorianus*. 11. Scolex. 12. Genitalia of mature segment. 13. Premature segment following patency of genital atria and filling of seminal receptacles, but with male and female genitalia poorly developed. 14. Mature segment. 15. Pregravid segment. Scale bars = 0.1 mm.

wide, velum 0.35 – 0.64 (0.48, n = 5) long. Genital pores paired, in middle of lateral segment margins. In premature segments, genital atrium circular in dorso-ventral views, not patent; in mature segments, genital atrium consists of narrow central passage with numerous anterior and posterior diverticula. Cirrus sac elongate, with thick muscular wall, extending just beyond osmoregulatory canals into medulla; cirrus sac wider near proximal extremity; 0.70 – 0.86 (0.78, n = 5) long by 0.16 – 0.24 (0.20, n = 5) wide in mature segments, 0.92 – 1.09 (0.97, n = 5) long by 0.23 – 0.25 (0.24, n = 5) wide in pregravid segments. Distal cirrus greatly dilated, armed with numerous, regularly-arranged spines, 0.008 long; proximal cirrus narrow, coiled, with reduction in size of spines; most proximal region of cirrus unarmed, leads to fusiform internal seminal vesicle 0.22 – 0.36 (0.27, n = 5) long by 0.11 – 0.17 (0.14, n = 5) wide in mature segments, 0.24 – 0.47 (0.35, n = 5) long by 0.16 – 0.20 (0.18, n = 5) wide in pregravid segments; cirrus sac between distal extremity and internal vesicle filled with densely-staining gland cells.

External seminal vesicle elongate, 0.27 – 0.55 (0.43, n = 5) by 0.09 – 0.12 (0.10, n = 5), extends medially and anteriorly from proximal pole of cirrus sac, along anterior border of seminal receptacle; covered with layer of glandular cells; vas deferens arises from proximal pole of external seminal vesicle. Testes invariably arranged in two completely separate groups 30-57 (39, n = 5) per group, extending from ventral osmoregulatory canals to level of medial part of seminal receptacle; 1 to 4 rows of testes in antero-posterior direction; at least 2 layers in dorso-ventral plane; testis diameter 0.050 – 0.080 (0.060, n = 10). Vagina tubiform, opening to genital atrium posterior to cirus sac; connection between vagina and genital atrium clearly visible in premature segments prior to patency of genital atrium; once genital atrium becomes patent, distal vagina atrophies and becomes inapparent. Vagina leads to ovoid seminal receptacle 0.32 – 0.44 (0.37, n = 5) by 0.19 – 0.28 (0.24, n = 5), on posterior margin of segment medial to cirrus sac; receptacle empty prior to patency of genital atrium, filled with sperm immediately genital atrium becomes patent. Ovary flabelliform, 0.24 – 0.43 (0.30, n = 5) by 0.43 – 0.57 (0.53, n = 5), with oöcapt near medial pole of seminal receptacle; ovary on ventral aspect of medulla. Vitellarium horseshoe-shaped, 0.14 – 0.20 (0.16, n = 5) by 0.23 – 0.27 (0.25, n = 5), posterior and dorsal to ovarian isthmus. Mehlis' gland spherical, 0.09 – 0.13 (0.11, n = 5) in diameter, situated in U of vitellarium. Uterus paired in each segment, situated anterior to ovaries; immature uterus tubiform, extending laterally to proximal poles of cirrus sacs; in pregravid segments, uterus develops numerous anterior and posterior diverticula, crosses osmoregulatory canals dorsally, extending to postero-lateral margins of segments. No gravid specimens present; eggs in all available specimens immature. Paired osmoregulatory canals present; ventral canal larger, 0.080 – 0.150 in diameter in mature segments, 0.140 – 0.310 in postmature segments; dorsal canal external to ventral, much narrower, 0.020 – 0.060 in diameter in mature segments, 0.040 – 0.050 in diameter in postmature segments; tiny accessory canals, 0.020 in diameter visible in some segments, medial to ventral canal; transverse canal connects ventral canals at posterior margin of each segment, diameter 0.020 – 0.060; tiny canal connecting dorsal canals 0.012 in diameter. Development of segments in largest specimen: genitalia formed but immature by segment 65; genital atrium becomes patent in segment 70; sperm appear in seminal receptacle in segment 73; first mature segment 95; uterus commences filling in segment 110; ovary involuted with remnants of vitellarium still present by segment 150; total number of segments 225.

Remarks

Progamotaenia wallabiae was described by Beveridge (1985) based on three specimens from the grey scrub wallaby, *Dorcopsis luctuosa* (D'Albertis, 1874) (= *D. veterum* (Lesson & Garnot, 1826) in Spratt *et al.* 1991) from Papua. Because the species was described from such a limited series of specimens and because its occurrence in the tree kangaroo, *D. dorianus*, involves a different host genus, a description of the specimens is provided. The occurrence of the species in *D. dorianus* was first reported by Flannery *et al.* (1996) and the description presented here is based on the specimens from the latter report.

The new specimens are not gravid, but do not differ significantly from the original specimens. The internal seminal vesicle is apparently larger than in the original description, but all other measurements conform closely with the description of *P. wallabiae*. Beveridge (1985) noted that the broad velum was undulate, with about 20 small lobes. In the new material, there are 30-35 distinct lobes on each side of the velum. Their arrangement is distinctive in that only the tips of the lobes are separated, while the divisions extend anteriorly into the velum without separation of the component lobes. This feature is unique within the genus as species have either a straight-edged velum or a velum split into prominent triangular or linguiform lobes. In the case of *P. thylogale*, the velum is scalloped, but there are no thickenings or divisions extending anteriorly beyond the edge. The feature described above may be characteristic of the species.

Discussion

The descriptions of cestodes of the genus *Progamotaenia* presented above suggests that tree kangaroos, while not harbouring a helminth fauna as diverse as some other macropodid genera, possess nevertheless distinctive species of cestodes. Descriptions are limited by the difficulty in obtaining material and by the fact that material obtained can rarely be preserved in an ideal manner. Nevertheless, it is possible to identify species and provide adequate descriptions of them from the material available. Notwithstanding the obvious limitations, some conclusions can be drawn on the species of *Progamotaenia* found in tree kangaroos.

Progamotaenia dendrolagi sp. nov. is found in both of the Australian species of tree kangaroos, *D. lumholtzi* and *D. bennettianus*, but has not, thus far been found in species in New Guinea. The Australian species of tree kangaroos are closely related phylogenetically (Flannery *et al.* 1996; Bowyer *et al.* 2003) and may either represent a recolonisation by the genus from New Guinea

(Winter 1997) or an endemic Australian phylogenetic lineage (Bowyer *et al.* 2003). The phylogenetic affinities of *P. dendrolagi* are not clear as the (intestinal) species which it most closely resembles, *P. ewersi*, is highly distinctive morphologically. In the absence of a formal phylogenetic analysis of the genus *Progamotaenia*, the affinities of *P. dendrolagi* are difficult to infer. It is apparently highly host specific as the species has not been found in other macropodids in north-eastern Queensland (Beveridge *et al.* 1989, 1992, 1998). Given the uncertainty as to the phylogenetic affinities of the cestode, its associations warrant further investigation and may provide significant insights into the mode of evolution of cestodes of macropodids.

Progamotaenia irianensis sp. n. was first reported as *P.* cf *dorcopsis* (see Flannery *et al.* 1996) based on the presence of a prominently fimbriated velum, two uteri and the testes distributed in two distinct groups. The more detailed study presented here indicates that it is in fact a new species based on the number and shape of the elements of the velum. It has only been found in *D. dorianus* at a single locality in the mountains of Irian Jaya. The helminths of other macropodids occurring in the area are completely undocumented and therefore it is not possible to exclude the hypothesis that the species occurs commonly in other macropodids and may therefore not be primarily a parasite of tree kangaroos. The scrub wallabies which occur in the same general region, *Dorcopsis muelleri* (Schlegel, 1866) and *Dorcopsulus vanheurnei* (Thomas, 1922), should therefore also be considered as potential alternative hosts.

Progamotaenia wallabiae was first reported from *Dorcopsis luctuosa* from Papua (Beveridge 1985). The host reported in the original description was *D. veterum*, but this species was subsequently considered a *species inquirenda* by Groves & Flannery (1989). They indicated that the appropriate name for the scrub wallaby from the Port Moresby region was *D. luctuosa*. It may be that *P. wallabiae* is more widely distributed in species of *Dorcopsis*, than currently indicated by published records, and infects tree kangaroos which occur in sympatry with various species of scrub wallabies. However, the host and geographical distributions of the species are too poorly understood to allow conclusions to be drawn. The occurrence of *P. wallabiae* in tree kangaroos and scrub wallabies in New Guinea provides a striking contrast with *P. dendrolagi* in Australia which is apparently highly host specific and occurs only in tree kangaroos.

All species of anoplocephaline cestodes whose life cycles have been fully elucidated utilise oribatoid mites as intermediate hosts (Denegri 1993). No life cycles of species of *Progamotaenia* have been elucidated. However, in the case of species of the related cestode genus *Bertiella* Stiles & Hassall, 1902 occurring in Australian possums (*Trichosurus* spp.), also an arboreal mammal, the initial development of metacestodes has been observed in oribatid mites (Viggers & Spratt 1995) and therefore it seems likely that species of *Progamotaenia* may also utilise oribatoids as intermediate host. If this is the case, the life cycle is essentially terrestrial as the mites are common in soil and pastures (Denegri 1993). The most extensively studied species of *Dendrolagus* are the Australian species, *D. bennettianus* and *D. lumholtzi*. *D. lumholtzi* spends 99% of its time in the tree tops and together with *D. bennettianus*, subsists primarily on the leaves of rainforest trees and vines (Flannery *et al.* 1996). Consequently, the only opportunity for tree kangaroos to become infected with cestodes occurs when they feed on the ground and accidentally ingest mites which are infected with the intermediate stages (cysticercoids) of the parasites. This implies that they must feed on the ground in areas where faeces containing cestode eggs have fallen and consequently infected the local mite population. Given the biological features of the hosts, it is remarkable that they are infected by any anoplocephalid cestodes. Alternatively, the current studies of host biology may have underestimated the extent to which the kangaroos feed on the ground. Unpublished observations (PMJ) suggest that in contrast to the published data, both *D. bennettianus* and *D. lumholtzi* spend a substantial amount of time on the ground. Were they to feed consistently on the ground in areas in which species of *Dorcopsis* also occur, then a ready explanation could be provided for the occurrence of *P. wallabiae* in *D. dorianus*. More extensive studies both of the occurrence of parasites in tree kangaroos as well as of host biology are needed before the various questions posed by the present study can be resolved.

Acknowledgements

Our thanks are due to Tim Flannery and Dave Spratt for providing specimens for the current paper and to Dave Spratt for commenting on a draft of the manuscript. The work was supported financially by the Australian Biological Resources Study.

References

BEVERIDGE I. (1976) A taxonomic revision of the Anoplocephalidae (Cestoda: Cyclophyllidea) of Australian marsupials. *Aust. J. Zool. Suppl. Ser.*, **44**, 1-110.

________ (1978a) A taxonomic revision of the genera *Cittotaenia* Riehm, 1881, *Ctenotaenia* Railliet, 1893, *Mosgovoyia* Spasskii, 1951 and *Pseudocittotaenia* Tenora, 1976. *Mém. Mus. Natn. Hist. Nat., Sér. A, Zool.* **107**, 1-64.

________ (1978b) *Progamotaenia ruficola* sp.n. (Cestoda: Anoplocephalidae) from the red kangaroo, *Macropus rufus* (Marsupialia). *J. Parasitol.* **64**, 273-276.

________ (1980) *Progamotaenia* Nybelin (Cestoda: Anoplocephalidae) : new species, redescriptions and new host records. *Trans. R. Soc. S. Aust.* **104**, 67-79.

________ (1985) Three new species of *Progamotaenia* (Cestoda: Anoplocephalidae) from Australasian marsupials. *Syst. Parasitol.* **7**, 91-102.

________ (1994) Family Anoplocephalidae Cholodkowsky, 1902. pp. 315-366 *In* Khalil, L.F., Jones, A., Bray, R.A. (Eds) "Keys to the Cestode Parasites of Vertebrates". (CAB International, Wallingford).

________, CHILTON N. B., JOHNSON P. M., SMALES L. R., SPEARE R. & SPRATT D. M. (1998) Helminth communities of kangaroos and wallabies (*Macropus* spp. and *Wallabia bicolor*) from north and central Queensland. *Aust. J. Zool.* **46**, 473-495.

________, SPEARE R., JOHNSON P. M. & SPRATT D. M. (1992) Helminth parasite communities of macropodoid marsupials of the genera *Hypsiprymnodon*, *Aepyprymnus*, *Thylogale*, *Onychogalea*, *Lagorchestes* and *Dendrolagus* from Queensland. *Wildl. Res.* **19**, 359-376.

________ & SPRATT D. M. (1996) The helminth fauna of Australasian marsupials: origins and evolutionary biology. *Adv. Parasitol.* **37**, 136-254.

________, SPRATT D. M., CLOSE R. L, BARKER S. C. & SHARMAN G. B. (1989) Helminth parasites of rock-wallabies, *Petrogale* spp. (Marsupialia), from Queensland. *Aust. Wildl. Res.* **16**, 273-287.

________ & THOMPSON R. C. A. (1979) The anoplocephalid cestode parasites of the spectacled hare-wallaby, *Lagorchestes conspicillatus* Gould, 1842 (Marsupialia: Macropodidae). *J. Helminthol.* **53**, 153-160.

________ & TURNI C. (2003) *Progamotaenia capricorniensis* sp. nov. (Cestoda: Anoplocephalidae) from wallabies (Marsupialia: Macropodidae) from Queensland, Australia. *Parasite* **10**, 309-315.

BOWYER, J. C., NEWELL, G. R., METCALFE, C. J. & ELDRIDGE, M. B. D. (2003) Tree-kangaroos *Dendrolagus* in Australia: are *D. lumholtzi* and *D. bennettianus* sister taxa? *Aust. Zool.* **32**, 207-213.

DENEGRI, G. (1993) Review of oribatid mites as intermediate hosts of tapeworms of the Anoplocephalidae. *Exp. Appl. Acarol.* **17**, 567-580.

FLANNERY, T.M., MARTIN, R. & SZALAY,A. (1996) Tree kangaroos : a curious natural history. (Reed Books ; Melbourne).

GROVES, C. P. & FLANNERY, T. F. (1989) Revision of the genus *Dorcopsis* (Macropodidae: Marsupialia) pp. 117-128. *In* Grigg, G, Jarman, P.& Hume, I (Eds) "Kangaroos, wallabies and rat-kangaroos" (Surrey Beatty & Sons, Chippimg Norton).

LÖSER, E. (1965) Der Feinbau des Oogentop bei Cestoden. *Z. Parasitenkde* **25**, 413-458.

PRITCHARD, M. H. & KRUSE, G. O. W. (1982) The Collection and Preservation of Animal Parasites. (University of Nebraska Press, Lincoln).

SPRATT, D. M., BEVERIDGE, I. & WALTER, E. L. (1991) A catalogue of Australasian monotremes and marsupials and their recorded helminth parasites. *Rec. S. Aust. Mus. Monogr. Ser.* **1**, 1-105.

SCHMIDT, G. D. (1986) "CRC Handbook of Tapeworm Identification". (CRC Press, Boca Raton).

TURNI, C. & SMALES, L. R. (1999) *Progamotaenia abietiformis* sp. nov. (Cestoda: Anoplocephalidae) from *Onychogalea fraenata* (Marsupialia: Macropodidae) from central Queensland. *Trans. R. Soc. S. Aust.* **123**, 143-147.

WINTER, J. W. (1997) Response of non-volant mammals to Late Quaternary climatic changes in the Wet Tropics region of north-eastern Australia. *Wildl. Res.* **24**: 493-511.

VIGGERS, K. L. & SPRATT, D. M. (1995) The parasites recorded from *Trichosurus* species (Marsupialia : Phalangeridae). *Ibid.* **22**, 311-332.